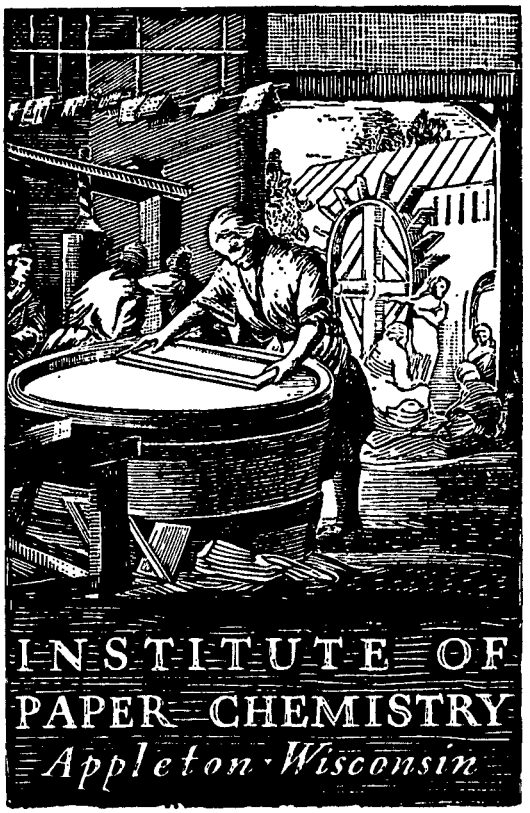

METHODS FOR MEASURING PRIMARY PRODUCTIVITY IN AQUATIC ECOSYSTEMS

Project 3355

Report Six
A Progress Report
to
MEMBERS OF THE INSTITUTE OF PAPER CHEMISTRY

September 10, 1982

THE INSTITUTE OF PAPER CHEMISTRY

Appleton, Wisconsin

METHODS FOR MEASURING PRIMARY PRODUCTIVITY IN AQUATIC ECOSYSTEMS

Project 3355

Report Six

A Progress Report

to

MEMBERS OF THE INSTITUTE OF PAPER CHEMISTRY

September 10, 1982

TABLE OF CONTENTS

LIST OF TABLES

THE INSTITUTE OF PAPER CHEMISTRY

Appleton, Wisconsin

METHODS FOR MEASURING PRIMARY PRODUCTIVITY IN AQUATIC ECOSYSTEMS

SUMMARY

Project 3355 was a multicomponent project designed to evaluate the methods and techniques used to measure and monitor impacts of papermaking effluents on aquatic receiving streams. This report is a compilation and critical review of the methods available for the measurement of planktonic and algal primary productivity. In it we discuss some strengths and weaknesses of the methods currently available and their applicability to the requirements and characteristics of papermaking effluents.

The methods available can be grouped into 4 categories:

a. Methods based on rates of change in algal biomass

b. Methods for nonisolated communities

c. Methods based on isolated communities

d. Mathematical modeling techniques

The most widely used technique has been to measure changes in biomass using weight, volume, cell counts, and ATP and chlorophyll pigment analysis. Each of these parameters requires slightly different sampling methods. At the present time, the sampling method most widely used and most useful for measuring periphyton biomass is the glass slide artificial substrate.

Changes in nonisolated communities are most often identified by measuring changes in chemical composition of the water. The variables most often used are oxygen and CO_2. This approach can give information on long- and short-term fluctuations under several ambient conditions. However, this methods lacks precision because conditions of water movement and animal interactions cannot be controlled.

Isolated community methods (such as light and dark bottle tests) are short-term tests within limited parameters. This technique has also been used with measurements of incorporation of radioactive carbon as the determining variable. Even with its limitations and complexity, the ^{14}C method is most sensitive and remains as the only satisfactory method available for measuring productivity in oligotrophic waters.

Mathematical approaches include modeling to make predictions based on easily measured variables such as light intensity, temperature, chlorophyll, and nutrients. Modeling allows comparisons of river and lake systems over a reasonable time frame that could otherwise not be measured. Modeling, however, requires an effort that may not be feasible for many applications of primary productivity data.

INTRODUCTION

The primary productivity of algae has received a great deal of attention from limnologists and has been measured in detail in a number of aquatic systems. The principal reason for this is that the rate and amount of carbon fixed at the primary producer level can determine the amount of matter and energy available for transfer and use at higher trophic levels. In large lakes and rivers, planktonic productivity often represents the dominant input of new organic matter and potential energy that drives the system. In smaller bodies of water and headwater streams, energy is derived from autotrophic production and allochthonous sources as well.

Impacts that alter rates of primary production can affect the transfer of energy to higher trophic levels, thus changing the productive capacity of the ecosystem. Consequently, to understand more clearly the changes that might occur, it is important that results of productivity analyses be comparable among different ecosystems, among different community components of the same system, and among similar components responding to natural or perturbed conditions. In spite of this obvious need, a great diversity exists in the presentation of results. Much of this disparity is related to the choice of study methods employed.

The process of photosynthesis can be summarized in the following equation:

$$\underset{(A)}{6CO_2 + 12\ H_2O} \xrightarrow[\text{pigment}\ \text{receptor}]{\text{light}} \underset{(B)}{C_6H_{12}O_6} + 6H_2O + \underset{(C)}{6O_2} \qquad (1)$$

Although this equation is a gross oversimplification of the entire metabolic process, it does show those areas (A, B, C) upon which current methods are based for measuring aquatic primary productivity. Productivity estimates can be made from measurements of changes in pH (A), carbon dioxide (A), carbon uptake (B), biomass accumulation (B), or oxygen production (C). Measurements can be made in the natural

environment (in situ) on nonisolated communities or on isolated samples of natural communities, which are incubated at the points of collection or under simulated natural conditions. However, since each method measures the rate of different reactions (A, B, or C), results may not always be comparable. Since we know the approximate relationship of oxygen evolution to carbon reduction and carbohydrate formation [Eq. (1)], it is possible to make conversions between any of the various equivalent parameters of production (Table I). However, these are subject to error and should be used only as a last resort (Winberg, 1960).

TABLE I

PHYTOPLANKTON EQUIVALENTS CALCULATED ACCORDING TO THE BALANCED PHOTOSYNTHETIC EQUATION

	O_2		CO_2		C
	mg	mL	mg	mL	mg
1 mg O_2	--	0.700	1.375	0.700	0.375
1 mL O_2	1.429	--	1.965	1.000	0.536
1 mg CO_2	0.727	0.509	--	0.509	0.273
1 mL CO_2	1.429	1.000	1.965	--	0.536
1 mg C	2.667	1.866	3.667	1.866	--

Adapted from Winberg (1960) and Lind (1974).

Important to the understanding of production is an understanding of the terms used. Primary production is the quantity of new organic matter created by photosynthesis. Primary productivity is the rate at which production occurs (hour^{-1}, day^{-1}, month^{-1}, etc.). Gross productivity is the rate of production of new organic matter including that subsequently used and lost during the time interval as a result of nonpredatory losses (respiration, excretion and secretion, death or injury) and predatory losses (grazing). Net productivity is the gross rate of accumulation of new organic matter minus losses.

The intent of this report is to provide the analyst with enough information about methods for measuring aquatic primary productivity so that sound decisions can be made in selecting the appropriate method. A detailed step-by-step discussion of each method is beyond the scope of this report. More thorough discussions can be found in reviews by Vollenweider (1974), Strickland and Parsons (1972), McAllister et al. (1964), and Winberg (1960).

The information presented in this report is divided into four major sections which provide a review and evaluation of the methods currently utilized to estimate the productivity of phytoplankton and periphyton assemblages: (1) methods based on the measurement of rates of changes in algal biomass (2) methods for nonisolated communities (3) methods based on isolated communities, and (4) mathematical modeling techniques.

MEASUREMENT OF PRIMARY PRODUCTION RATES FROM CHANGES IN BIOMASS

Estimates of aquatic primary productivity based on measurements of changes in algal biomass were the first methods employed. In practice, the increase or decrease in the standing crop of algae over a measured interval of time can provide a crude estimate of primary productivity. However, rates of primary production based on a temporal set of biomass measurements reflect only minimal estimates or underestimations of net productivity as a result of losses from grazing, current transport, sedimentation, death, and decomposition (Ryther, 1956; Goldman, 1968; Vollenweider, 1974; Wetzel, 1975; Verduin, 1956). For aquatic macrophytes and periphyton communities, productivity can be estimated rather well from changes in biomass over time. Changes in phytoplankton communities, in general, are more difficult to analyze.

Numerous methods have been used to measure the biomass of algal communities upon which estimates of primary productivity are based, including enumeration, volume, wet weight, dry weight, organic weight, chlorophyll pigments, and ATP. Often these methods have been employed uncritically, which makes comparisons and interpretation difficult (Vollenweider, 1974; Wetzel, 1975). Nevertheless, if rates of primary production are to be calculated from biomass changes, then several basic requirements must be fulfilled.

(1) Frequency of sampling material should be short, not to exceed one week.

(2) Algae distribution must be fairly homogeneous.

(3) There should be no significant losses resulting from grazing, sedimentation, and transport.

As alluded to earlier, estimates of primary production from changes in phytoplankton biomass are subject to many uncertainties. The distribution of phytoplankton is rarely, if ever, homogeneous in the water column, and it is not always possible to account for all the losses (predatory and nonpredatory). In spite of these problems, methods have been developed to estimate daily primary production from biomass measurements.

The earliest attempts at estimating the productivity of phytoplankton from biomass measurements were based solely on changes in the number of organisms (Ryther, 1956; Verduim, 1956; Goldman, 1968; Vollenweider, 1974; Wetzel, 1975). This provided quite a biased estimate of biomass and production because of the great difference in size among algae. In addition, plankton nets of fairly large mesh size were often used, in which significant portions of the algae were not retained. Vollenweider (1974) suggests that if this method is to be used, it is best to collect samples from a series of sampling stations located within the study area from various depths

at each station. Biomass changes, expressed as the average daily increase or decrease, between two consecutive observations can then be calculated.

Greatest success in estimating phytoplankton productivity has been achieved by using measurements of chlorophyll concentration and its relationship to light intensity (chlorophyll-light technique) (Ryther and Yentsch, 1957, 1958; Small et al., 1972; Soltero and Wright, 1975). Ryther and Yentsch (1957, 1958) developed methods to predict daily primary production based on photosynthetic responses to incident light and measured chlorophyll concentration. In addition, revisions of the original method have been made to account for heterogeneous distributions and water temperature (Small et al., 1972; Soltero and Wright, 1975).

The chlorophyll-light technique requires data on:

(1) The average chlorophyll a concentration of the euphotic zone

(2) Total solar radiation

(3) The extinction coefficient of the water column

It is assumed that for every gram of chlorophyll a, 3.7 grams of carbon are assimilated per hour at light saturation. This procedure has been tested against ^{14}C measurements (to be discussed later) with very good results (Ryther and Yentsch, 1958; Small et al., 1972). Nevertheless, this technique is not without its critics (Steemann-Nielsen, 1964). Most critics state that the light-saturated rate of photosynthesis for a given concentration of chlorophyll may vary by more than a factor of 10, making this technique unsuitable for measuring primary production.

Estimates of periphyton productivity were first derived from the measurements of the rate of accumulation of biomass on artificial substrates (Bridge-Cooke, 1956; Waters, 1961; Kevern et al., 1966; King and Ball, 1966; Clark et al., 1979; Rogers et al., 1980). The biomass accumulating on a known area of substrate within

a given time period is a measure of approximate net production rates. This method has been accurate in situations where colonization is relatively rapid and the incubation period is primarily a period of instantaneous growth (Kevern et al., 1966). In similar analyses, the amount of chlorophyll a has been used for estimates of primary productivity (Waters, 1961). Although methods for measuring rates of periphyton production based on the colonization of artificial substrates is subject to error (Bridge-Cooke, 1956; King and Ball, 1966; Clarke et al., 1979), this approach is useful in view of the heterogenous distribution of periphyton on natural substrates (Vollenweider, 1974). This approach is also useful in that the production values obtained are readily comparable.

MEASUREMENTS OF PRIMARY PRODUCTIVITY OF NONISOLATED ALGAL COMMUNITIES

In moderate to highly productive aquatic ecosystems it is feasible to measure short-term fluctuations in the chemical composition of the water that result from the metabolic activities of the aquatic plant and animal communities. Often there are appreciable diurnal variations in dissolved oxygen and carbon dioxide concentrations, and there may also be measurable changes in essential plant nutrients (phosphorus, nitrogen, silica). In principle, the changes that occur in the natural environment (in situ) can be used to estimate primary productivity.

Methods developed for making in situ measurements of primary productivity are similar for both lentic and lotic ecosystems (see Vollenweider, 1974). From Eq. (1), we assume that as each mole of carbon dioxide is reduced during photosynthesis, a mole of oxygen is released to the water. If corrections can be made for the diffusion of oxygen across the air-water interface, this method can be used to estimate the rate at which the community is incorporating CO_2 (Odum, 1956, 1957; Duffer and Dorris, 1966; Schindler et al., 1973). By making measurements over a 24-hour period, the decrease in oxygen during darkness can be determined, making it possible to

estimate community respiration. Similarly, productivity estimates can be made by measuring changes in the concentration of carbon dioxide (Ryther, 1956; Goldman, 1968; Vollenweider, 1974).

In waters of alkaline pH, CO_2 exists in equilibrium with HCO_3^- and $CO_3^{=}$ (the carbonate-bicarbonate buffer system). As CO_2 is removed from an aquatic system during photosynthesis, the pH rises. Thus, by measuring changes in pH over a 24-hour period it is possible to estimate both photosynthesis and respiration (Schindler et al., 1973). Because of the buffering capacity of many fresh waters, a relatively large uptake of CO_2 is necessary to produce a significant change in pH. Hence, in lakes with a high alkalinity, a detectable pH change within 24 hours will occur only in areas of high production.

The depletion of major plant nutrients (phosphorus, nitrogen) in the water over long periods has been used in the past to estimate primary production (Ryther, 1956; Goldman, 1968; Vollenweider, 1974). However, results from these studies are difficult to interpret quantitatively because of the problem in accounting for the regeneration and reutilization of these substances over the study period. In addition, the relationship between the concentration of various nutrients and the production of organic matter is extremely variable.

There are several advantages in making in situ measurements of primary productivity. Communities are not enclosed (isolated); measurements are made under natural conditions including both planktonic and attached vegetation. It is difficult in an enclosure to reproduce natural conditions (turbulence, light radiation, nutrient renewal); hence, rates of metabolism often differ. Observations in situ can be continued over long periods, whereas experiments in enclosures are limited in duration by excessive changes in metabolic by-products, nutrient depletion, and

bacterial growth. Another advantage of this method is the estimate one gets of community respiration.

In spite of the above advantage this approach has considerable limitations. The overall precision of productivity measurements made by these techniques is not generally great because of uncertainties in the corrections for diffusion and water movements. Only gross primary production can be estimated directly, since the measurements of respiration include the entire community (plant and animal). Possible errors also result from short-term fluctuations in the rates of oxygen consumption and atmospheric exchange coefficients that are difficult to assess.

MEASUREMENT OF PRIMARY PRODUCTIVITY USING ISOLATED ALGAL COMMUNITIES

Many of the problems encountered in making estimates of primary productivity on nonisolated algal communities can be reduced by making measurements on samples which have been enclosed in glass bottles long enough for measurable changes to occur. In practice, the changes in oxygen production or rates of carbon uptake are measured on isolated samples of natural algal communities which are incubated for brief periods at the points of collection (in situ) or under simulated natural conditions in the laboratory. During the incubation period, temperature and light are simulated closely, whereas other environmental factors such as turbulence, nutrient replenishment, and grazing can differ to varying degrees in the isolated samples.

The light and dark bottle approach for measuring primary productivity was first employed in the mid-1920's and since then has received wide application (see Goldman, 1968). The two most commonly employed techniques measure either oxygen production (O_2 method) or carbon assimilation (^{14}C method) (Table II). Both approaches can be applied to phytoplankton and periphyton populations; however, for periphyton studies modification of the techniques is required.

TABLE II

A COMPARISON OF THE ^{14}C and O_2 METHODS OF MEASURING PRIMARY PRODUCTIVITY

	^{14}C Method	O_2 Method
Light chamber	^{14}C - CO_2 Assimilated	O_2 Produced
Dark chamber	^{14}C - CO_2 Assimilated (heterotrophic uptake)	O_2 Consumed (respiration)
Sensitivity	0.05 mg C $m^{-3}hour^{-1}$	2-3 mg C $m^{-3}hour^{-1}$
Limitations	-no satisfactory way to measure respiration	-must assume respiration is the same in both chambers
	-uncertainty as to whether method measures net or gross photosynthesis	-interferences (COD, heterotrophic respiration, Fe) affect accuracy of DO estimates
	-loss of soluble organic products formed during photosynthesis	-limited sensitivity

In the O_2 method, the amount of oxygen evolved during photosynthesis is used as a measure of the rate of primary production [see Eq. (1)]. When samples of phytoplankton populations are incubated in a depth profile in clear (light) and opaque (dark) bottles, the initial concentration of dissolved oxygen (C_1) can be expected to decrease to a lower level (C_2) in the dark bottle as a result of respiration, and to be changed to another value (C_3) in the light bottle as a result of photosynthetic activity and respiration. With these measurements, photosynthetic production can be determined as follows:

- C_1-C_2, represents the respiratory activity over the time interval involved
- C_3-C_1, represents the net photosynthetic activity
- C_3-C_2, represents the gross photosynthetic activity

Several assumptions are made in this method that can alter the photosynthetic measurements appreciably (Strickland and Parsons, 1972; Vollenweider, 1974; Wetzel,

1975). Respiration rates are not necessarily the same in light and dark. Since photorespiration occurs in algae, other processes utilize oxygen separately from respiratory uptake. In addition, it must be assumed that the oxygen uptake by bacteria and other animals is negligible. However, this is rarely known. Under most circumstances, these errors are small, but the technique can be considered only as a reasonable estimate. It is likely that these as well as analytical errors in determination of oxygen concentrations are less than sampling errors of heterogeneous plankton populations (Cassie, 1962; Wetzel, 1975).

Photosynthetic rates can similarly be determined in light-dark bottles by measuring the incorporation of radioactive carbon in the organic matter of algae after a short incubation period. This method was first introduced by Steemann-Nielsen in 1952 (see Steemann-Nielsen, 1964), and since then has been modified and refined through continuous use (Strickland and Parsons, 1972; Vollenweider, 1974; Gieskes et al., 1979; Peterson, 1980). This procedure involves the addition of radiocarbon, usually in the form of ^{14}C-labeled $NaHCO_3$, to samples of water. It is assumed that the radioisotope added to the sample containing an algal population is assimilated at the same rate as the corresponding nonlabeled compound occurring naturally in the water. After incubation in the same manner as described for the O_2 method, the samples are filtered, and the radiocarbon content of the particulate matter is assayed by one of several instruments that detect β radiation. Both Geiger-Müller planchet counters (Strickland and Parsons, 1972; Vollenweider, 1974) and liquid scintillation spectrometers (Lind and Campbell, 1969; Pugh, 1970) are commonly used.

It is believed that measurements using this technique approximate net primary productivity; however, this is still subject to debate (Steemann-Nielsen, 1964; Peterson, 1978, 1980; Gieskes et al., 1979). The method is sensitive and relatively

easy to use (Table II), but it is moderately expensive when considering the equipment needed to detect β radiation.

Despite the widespread use of this method in fresh and marine waters, a number of errors can affect its accuracy and precision and introduce bias into estimates of photosynthetic rates:

- Leakage of labeled carbon from algal cells due to preservation and filtration procedures
- Failure to extrapolate radiocarbon counts to infinite thinness in planchet counting
- Nonbiological or nonphotosynthetic fixation of radiocarbon
- Release of ^{14}C-labeled extracellular metabolites and significant uptake of carbon in dark bottles by photosynthesizing populations

These and related problems are discussed by Vollenweider (1974) and Strickland and Parsons (1972).

The techniques described for measuring phytoplankton productivity can be applied equally well to periphyton assemblages with only minor modifications. In lentic systems, investigators have relied on artificial substrates, isolating them to estimate rates of production. A recent study has shown that artificial substrate methods underestimate productivity by as much as 95% (Loeb, 1981). Loeb (1981) developed an incubation chamber to measure primary productivity with minimal disturbance of the natural community. Others have also indicated the importance of examining natural communities (Bauld et al., 1979; Kairesalo, 1980).

In lotic ecosystem (rivers), primary production estimates based upon enclosing small samples of stream periphyton in bottles is suspect because of the absence of normal turbulence (Pennak and Lavelle, 1979). The continual movement of water in

streams and rivers renews essential materials and removes metabolic by-products. When isolating periphyton communities adapted to riverine systems, a flow regime within the chamber must be maintained that is similar to natural conditions; otherwise an incorrect estimate of production may result (McIntire and Phinney, 1965; Rodgers et al., 1978, 1980). Hynes (1970) states that "...only direct measurement of undisturbed periphyton in chambers in which the water is kept moving, offers any real hope of determining the primary production by periphyton..."

Although the light-dark bottle approach solves several of the problems encountered when making in situ measurements, problems unique to this technique also occur (Vollenweider, 1974; Andersen and Sand-Jensen, 1980).

- Reduction of water circulation and turbulence may alter photosynthetic rates.
- Photosynthetic activity may be modified as a result of light shock and/or excessive turbulence from the initial handling of the samples.
- Sample populations may diverge (by growth, decay, grazing) from the original population.
- The chemical composition of the enclosed water may be altered and modify rates of plant growth and photosynthesis.
- Alterations in the quality of light as a result of absorption and reflection at or in the walls of the bottles or enclosures may alter photosynthetic activity.

In spite of these limitations, this technique has received the greatest use and the ^{14}C method is by far the most sensitive technique and the only method suitable for measuring productivity in oligotrophic waters.

MODELING AQUATIC PRIMARY PRODUCTION - MATHEMATICAL APPROACHES

While in situ measurements of primary production provide important and useful information on the productive status of a natural aquatic ecosystem, the amount of effort required to collect enough data to make sound management decisions may make this approach impractical. The number of stations that can be processed in a day is far too small to provide synoptic information. Day-to-day variations of primary production are often so great that daily measurements are needed to reliably estimate annual or seasonal production rates. In addition, it is difficult to realistically extrapolate the results of in situ measurements to daily rates since incubation times are generally confined to only a short part of the daylight period.

As a result of these problems, in those instances where estimates of algal production are necessary but where circumstances prevent photosynthetic measurements, investigators have turned to mathematical models to predict and simulate changes in aquatic primary production (Fee, 1969, 1973a,b; Jassby and Platt, 1976; Smith, 1980). A mathematical model of primary production entails a mathematical description of the physical, chemical, and biological processes that affect an algal community in a given aquatic ecosystem. This description usually takes the form of a series of differential equations which are incorporated into a computer program used to predict or estimate the system state for a given set of conditions. Ideally, if in situ productivity could be estimated with sufficient precision from more easily measured variables (light intensity, chlorophyll a, nutrients, temperature, etc.), productivity data could then be collected with greater spatial and temporal resolution for the same amount of effort (Jassby and Platt, 1976). Most models examine phytoplankton productivity in lakes (Steel, 1962; Fee, 1937a,b; Smith, 1980); only one has been developed for periphyton communities in streams (McIntire, 1973).

Models of primary production are based upon the relationship between photosynthesis and light intensity (Steele, 1962; Fee, 1969, 1973a,b; Lehman et al., 1975). Development of the earliest models required the following data:

(1) The depth distribution of the in situ photosynthetic rate
(2) The short-term photosynthetic rate at optimal light intensity
(3) The extinction coefficient of the water body
(4) The time variation of radiation entering the water surface over the time interval of interest (usually a day)

These models were designed to give reasonably accurate estimates of daily photosynthesis with a minimum amount of field data. The more recent models take into account 3 and 4 above, phytoplankton biomass (measured as chlorophyll concentration), and the photosynthetic efficiency of phytoplankton (Bannister, 1974; Smith, 1980).

Model output can be used in a number of ways for environmental prediction and management. Estimates of primary production rates are required for assessing the productive status of a lake or other natural water body, determining the effect of nutrient loading, or dealing with watershed management problems and cultural eutrophication. The results of a model also provide information linking the phytoplankton to the functioning of the other parts of the ecosystem, especially with respect to the amount of energy available for transfer to higher trophic levels (Fee, 1973b). In addition, by considering all of the major variables influencing carbon uptake, a model provides a single number that has valuable comparative uses. Thus, the results of a model can be used to objectively compare the present condition with future situations to demonstrate the effect of remedial actions or of further deterioration.

REFERENCES

Anderson, J. M. and Sand-Jensen, K. 1980. Discrepancies between O_2 and ^{14}C methods for measuring phytoplankton gross photosynthesis at low light levels. Oikos 35:359-64.

Bannister, T. T. 1974. Production equations in terms of chlorophyll concentration, quantum yield, and upper limit to production. Limnol. Oceanogr. 19(1):1-12.

Bauld, J., Chambers, L. A., and Skyring, G. W. 1979. Primary productivity, sulfate reduction and sulfur isotope fractionation in algal mats and sediments of Hamelin Pool, Shark Bay, WA. Freshwater Res. 30:753-64.

Bridge-Cooke, W. 1956. Colonization of artificial bare areas by microorganisms. Bot. Rev. 22:613-38.

Cassie, R. M. 1962. Frequency distribution models in the ecology of plankton and other organisms. J. Anim. Ecol. 31:65-92.

Clark, J. R., Dickison, K. L., and Cairns, J., Jr. 1979. Estimating Aufwuchs biomass. Methods and measurements of periphyton communities: A review. ASTM STP 690. p. 116-41.

Duffer, W. R. and Dorris, T. C. 1966. Primary productivity in a southern Great Plains stream. Limnol. Oceanogr. 11(2):143-51.

Fee, E. J. 1969. A numerical model for the estimation of photosynthetic production, integrated over time and depth, in natural waters. Limnol. Oceanogr. 14:906-11.

Fee, E. J. 1973a. Modelling primary production in water bodies: A numerical approach that allows vertical inhomogeneities. Jour. Fish. Res. Bd. Can. 30(10):1459-73.

Fee, E. J. 1973b. A numerical model for determining integral primary production and its application to Lake Michigan. Jour. Fish. Res. Bd. Can. 30(10):1447-68.

Gieskes, W. W. C., Kraay, G. W., and Baars, M. A. 1979. Current ^{14}C methods for measuring primary production: Gross underestimate in oceanic waters. Netherlands Jour. of Sea Research 13(1):58-78.

Goldman, C. R. 1968. Aquatic primary production. Am. Zoologist 8:31-42.

Hynes, H. B. N. 1970. The ecology of running waters. Liverpool Univ. Press, Liverpool. 555 p.

Jassby, A. D. and Platt, T. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. 21(4):540-7.

Kairesalo, T. 1980. Comparison of *in situ* photosynthetic activity of epiphytic, epipelic and planktonic algal communities in oligotrophic lakes. Southern Finland, J. Phycol. 16:57-62.

Kevern, N. R., Wilhm, J. L., and Van Dyne, G. M. 1966. Use of artificial substrate to estimate the productivity of periphyton. Limnol. Oceanogr. 11:499-502.

King, D. L. and Ball, R. C. 1966. A qualitative and quantitative measure of Aufwuchs production. Trans. Amer. Microsc. Soc. 85:232-40.

Lehman, J. T., Botkin, D. B., and Likens, G. E. 1975. The assumptions and rationales of a computer model of phytoplankton population dynamics. Limnol. Oceanogr. 20(3):343-64.

Lind, O. T. and Campbell, R. S. 1969. Comments on the use of liquid scintillation for routine determination of ^{14}C activity in production studies. Limnol. Oceanogr. 14:787-89.

Loeb, S. L. 1981. An *in situ* method for measuring the primary productivity and standing crop of the epilithic periphyton community in lentic systems. Limnol. Oceanogr. 26(2):394-9.

McAllister, C. D., Shah, N., and Strickland, J. D. H. 1964. Marine phytoplankton photosynthesis as a function of light intensity: A comparison of methods. Jour. Fish. Res. Bd. Can. 21(1):159-81.

McIntire, C. D. 1973. Periphyton dynamics in laboratory streams: A simulation model and its implications. Ecol. Monographs 43(3):?.

McIntire, C. D. and Phinney, H. K. 1965. Laboratory studies of periphyton production and community metabolism in lotic environments. Ecol. Monographs 35:237-58.

Odum, H. T. 1956. Primary production in flowing waters. Limnol. Oceanogr. 1:103-17.

Odum, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. Ecol. Monogr. 27:55-112.

Pennak, R. W.; Lavelle, J. W. 1979. *In situ* measurement of net primary production in a Colorado mountain stream. Hydrobiologia 66(3):227-35.

Peterson, B. J. 1978. Radiocarbon uptake: Its relation to net particulate carbon production. Limnol. Oceanogr. 23:179-84.

Peterson, B. J. 1980. Aquatic primary productivity and the ^{14}C-CO_2 method: A history of the productivity problem. Ann. Rev. Ecol. Syst. 11:359-85.

Pugh, P. R. 1970. Liquid scintillation counting of ^{14}C-diatom material on filter papers for use in productivity studies. Limnol. Oceanogr. 15:652-5.

Rogers, J. H., Jr., Dickison, K. L., and Cairns, J., Jr. 1978. A chamber for *in situ* evaluations of periphyton productivity in lotic systems. Arch. Hydrobiol. 81(3):389-98.

Rogers, J. H., Jr., Dickison, K. L., and Cairns, J., Jr. 1980. A review and analysis of some methods used to measure functional aspects of periphyton. Reprints from Spec. Tech. Publ. 690, Am. Soc. for Testing and Materials.

Ryther, J. H. 1956. Photosynthesis in the ocean as a function of light intensity. Limnol. Oceanogr. 1:61-70.

Ryther, J. H. 1956. The measurement of primary production. Limnol. Oceanogr. 1:72-84.

Ryther, J. H. and Yentsch, C. S. 1957. The estimation of phytoplankton production in the ocean from chlorophyll and light data. Limnol. Oceanogr. 2:281-6.

Ryther, J. H. and Yentsch, C. S. 1958. Primary production of continental shelf waters off New York. Limnol. Oceanogr. 3(3):327-35.

Schindler, D. W.; Frost, V. E., and Schmidt, R. V. 1973. Production of epilithiphyton in two lakes of the experimental lakes area; Northwestern Ontario. Jour. Fish. Res. Bd. Can. 30:1511-24.

Small, L. F., Curl, H., Jr., and Gloosohenko, W. A. 1972. Estimates of primary production off Oregon using an improved chlorophyll - light technique. Jour. Fish. Res. Bd. Can. 29(9):1261-7.

Smith, R. A. 1980. The theoretical basis for estimating phytoplankton production and specific growth rate from chlorophyll, light and temperature data. Ecological Modelling 10:243-64.

Soltero, R. A. and Wright, J. C. 1975. Primary production studies on a new reservoir; Bighorn Lake - Yellowtail Dam, Montana USA. Freshwater Biol. 5:407-21.

Steel, J. H. 1962. Environmental control of photosynthesis in the sea. Limnol. Oceanogr. 7:137-50.

Steemann-Nielsen, E. 1964. Recent advances in measuring and understanding marine primary production. J. Ecol. (Suppl.) 52:119-30.

Strickland, J. D. H. and Parsons, T. R. 1972. A practical handbook of seawater analysis. Second edition, Fish. Res. Bd. Can. Bulletin 167:310.

Verduin, J. 1956. Primary production in lakes. Limnol. Oceanogr. 1:85-91.

Vollenweider, R. A., editor. 1974. A manual on methods for measuring primary production in aquatic environments. Int. Biological Program Handbook. Blackwell Scientific Publications. Oxford, London. 225 p.

Waters, T. F. 1961. Notes on the chlorophyll method of estimating the photosynthetic capacity of stream periphyton. Limnol. Oceanogr. 6:486-8.

Wetzel, R. G. 1975. Limnology. W. B. Saunders Co. 743 p.

Winberg, G. G. 1960. Primary productivity of water. Book 1. A.E.C. -tr-5692:235.

THE INSTITUTE OF PAPER CHEMISTRY

Doyle Roarabaugh (EB)

Doyle B. Roarabaugh
Research Fellow
Aquatic Biology Group
Chemical Sciences Division

Eugene F Zanella

Eugene F. Zanella
Group Leader
Bio-Research Group
Chemical Sciences Division